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Developmental Variability (Pelagic and Benthic) in *Haminoea callidegenita* (Opisthobranchia: Cephalaspidea) is Influenced by Egg Mass Jelly

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Abstract. *Haminoea callidegenita* Gibson and Chia (1989) has a pattern of development similar to that of other lecithotrophic opisthobranchs, except for the stage at hatching. In this species, both veligers and juveniles hatch from each egg mass. The percent of each hatching stage was variable among masses, with most masses having 30 to 50% of total hatchlings emerging as veligers. Both veligers and juveniles emerge throughout the entire hatching period (lasting 3–11 days), although the percentage of veligers decreases during this period. Encapsulated embryos cultured without egg mass jelly had approximately 80% of the total hatchlings emerging as veligers. Separated embryos cultured in the presence of egg mass jelly pieces hatched with percentages of veligers similar to that observed in intact egg masses, suggesting the possibility of a diffusible compound present in the jelly mass that induces intracapsular metamorphosis. Egg mass jelly also induces metamorphosis in hatched veligers. A juvenile and adult food source (the green alga *Chaetomorpha linum*) induces extracapsular metamorphosis only.

Introduction

Opisthobranch molluscs are hermaphroditic with internal fertilization (Morton, 1979). As spawning occurs, fertilized eggs are enclosed either individually or in groups by membranous capsules that are then linked together to form strings within a gelatinous mass (Purchon, 1977). The development of a number of opisthobranch species has been described (Thompson, 1958, 1967; Rao, 1961; Smith, 1967; Chia, 1971; Bridges, 1975; Switzer-Dunlap and Hadfield, 1977; Bickell, 1978; Chia and Koss, 1978; Clark *et al.*, 1979; Williams, 1980; others). In all opisthobranch species that have been studied, there is an early phase of encapsulated development (benthic) followed by a veliger phase falling into one of three categories (Thompson, 1967): planktotrophic (feeding, pelagic veliger), lecithotrophic (non-feeding, pelagic veliger), and direct development (metamorphosis occurs within the egg mass, with the veliger stage either present or suppressed; Bonar, 1978).

Although it has been thought that each opisthobranch species has one type of development, at least a half-dozen species appear to be poecilogonous (reviewed by Bonar, 1978). The validity of poecilogony in these and other marine invertebrates is currently under discussion (Hoagland and Robertson, 1988). In opisthobranchs, developmental patterns may vary geographically (*Tenellia pallida* Alder and Hancock, Eyster 1979; *Elysia chlorotica* Gould, West *et al.*, 1984), with changing environmental conditions (such as food availability as in *Spurilla neapolitana*, Clark and Goetzfried, 1978), and simultaneously among individuals of one population (*Tenellia pallida*, Eyster, 1979).

Haminoea callidegenita is a cephalaspidean opisthobranch found in the San Juan Islands, Washington State. *H. callidegenita* has an unusual form of development which includes the hatching of both lecithotrophic veligers and juveniles from the same egg mass. In this paper, we describe it's larval development with emphasis on the hatching stage. Preliminary results indicate that the egg mass jelly contains a diffusible compound that promotes intracapsular metamorphosis.

Materials and Methods

Collection and maintenance

Adults and egg masses of *Haminoea callidegenita* were collected from Spencer's Spit, Lopez Island, Washing-

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ton, from June 1985 to April 1987. Spencer's Spit is a shallow lagoon (<1 m) with limited access to open water, influenced slightly by tidal cycles, and subject to wide fluctuations in temperature. The lagoon has a silty substratum and is dominated by the green alga *Chaetomorpha linum* (O. F. Mull.) Kutz and *Ulva* sp.

Adults and egg masses were maintained at Bamfield Marine Station, Bamfield, British Columbia (June 1985 to August 1986) and at the Department of Zoology, University of Alberta, Edmonton, Alberta, Canada (September 1986 to April 1987). Adults were maintained in glass aquaria with a continuous flow of seawater at ambient temperatures (6–12°C), and were supplied with *Chaetomorpha linum* and *Ulva* sp. as food. Egg masses were collected immediately after spawning and maintained in Pyrex dishes at either ambient seawater temperatures or 14–15°C. Culture water was replaced daily with bag-filtered (1 μm) seawater. Observations made on egg masses that were spawned in the laboratory were compared with those collected in Spencer's Spit. Newly hatched veligers and juveniles were removed daily and cultured as outlined for egg masses, with the addition of *Chaetomorpha* and *Ulva* as food in the case of the juveniles. Flakes of cetyl alcohol were added to reduce surface tension, thus decreasing the rate at which larval shells became trapped at the surface (Hurst, 1967). Antibiotics were not generally used. Cultures of veligers and/or juveniles were cleaned every second day. When juveniles reached approximately 3 mm in length (measured while they were actively crawling) they were transferred to partially submersed 500 ml beakers with vents of 335 μm Nitex mesh to provide a gentle but continuous flow of seawater, at temperatures of 12–15°C.

Light microscopic observations and measurements of embryonic, larval, and early juvenile stages were made using a calibrated ocular micrometer on a Reichert compound microscope or a Wild M5 microscope. Photomicrographs were taken using a Wild Photoautomat MPS 45 camera on a Wild compound microscope.

Induction of intracapsular metamorphosis

Developmental stage at hatching was determined by examining encapsulated embryos cultured: (1) within intact egg masses (n = 9 egg masses); (2) within egg masses sliced into approximately 2 mm thick segments (n = 10 slices, each from a different egg mass); and, (3) completely separated from the egg mass, with all remnants of the jelly mass removed (n = 10 cultures from different egg masses). The jelly layers were easily peeled away from the egg strings which were then opened to release the encapsulated embryos. The capsules were rinsed in filtered seawater to remove any possible remnants of jelly. Separated embryos were cultured under three conditions: (a) embryos only (n = 10 cultures, each containing embryos from a different egg mass); (b) embryos with *Chaetomorpha* (2 mg blotted wet weight *Chaetomorpha*/40 ml seawater, or 0.05 mg/ml; n = 10); and, (c) embryos with pieces of egg mass jelly floating in the culture water, but not in direct contact with the embryos (14 mg blotted wet weight jelly/40 ml seawater, or 0.35 mg/ml; n = 10). Embryos were cultured from early cleavage stages (0–2 days after oviposition) until hatching occurred (32–39 days after oviposition). Egg masses used were all produced by different females. All cultures were maintained at 14–15°C.

Sample sizes indicated above (n) represent the number of cultures per condition. Intact egg masses and slices were cultured individually per 100 ml jar. Separated embryos were maintained at densities of 50–60/jar. All jars contained 40 ml of bag filtered seawater. All cultures were cleaned every second day and maintained under the specified conditions until hatching occurred (approximately 32 days after oviposition). During the hatching period, each culture was examined daily and new hatchlings removed and counted.

Induction of extracapsular metamorphosis

Potential extracapsular metamorphic inducers were examined by providing veligers hatched from intact egg masses with one of several substrata on the day of hatching. Culture dishes (10 × 50 mm plastic petri dishes) were treated with Clorox (5% sodium hypochlorite) for 2 h, then triply rinsed and soaked in distilled water. Substrata provided were: (1) bag-filtered (1 μm) seawater only (control; n = 12 cultures); (2) filtered seawater plus *Chaetomorpha* (n = 7); (3) filtered seawater plus surface sediment (n = 7); and, (4) filtered seawater plus pieces of egg mass jelly (n = 15). Each culture dish contained five veligers. Observations were made at 12-h intervals until metamorphosis occurred or the veligers died (up to a maximum of 20 days after hatching). Culture dishes were not treated with Chlorox after the onset of the experiment. All cultures were maintained at approximately 20°C, a temperature commonly encountered during the summer months in the shallow lagoon at Spencer's Spit. All substrata were collected from the adult habitat.

Results

Oviposition and development

Adult *Haminoea callidegenita* were found in Spencer's Spit throughout the year. Viable egg masses were collected in all months except January and December. *H. callidegenita* egg masses were similar to Hurst's (1967) type D opisthobranch egg mass. They were short, thick cylinders, ranging from almost ovate (10 × 5 × 5 mm) to sausage shaped (36 × 6 × 6 mm). A typical mass produced by a 26 mm adult was 15 × 5 × 5 mm and

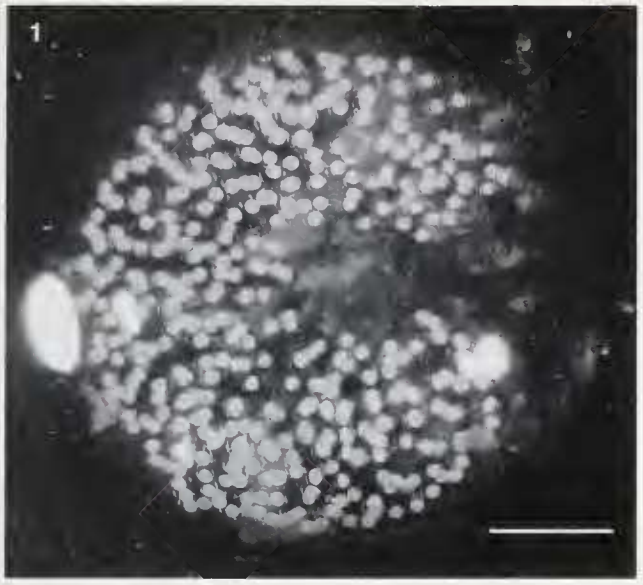

Figure 1. Photograph of a *Haminoea callidegenita* egg mass. Scale = 2 mm.

took approximately 20 min to be deposited. Egg masses were attached to the substrate along the length of one side, and were slightly curved in shape (Fig. 1), a result of the adult turning slightly towards the mass during oviposition. Adults did not show any substrate preference for oviposition and deposited masses on any available solid surface, both in the field and under laboratory conditions.

The bright orange-yellow eggs were individually encapsulated and arranged in a continuous string. This string spiralled through the periphery of the egg mass (irregularly deposited at a depth of approximately 1.5 mm) leaving the center and outer portion of the jelly free of embryos. Egg masses contained an average of 21 eggs/mm^3 egg mass (n = 10 masses), for a total of 200 to 700 eggs per mass. Density of eggs was variable within a single mass, as well as among masses. Uncleaved eggs measured 230 × 210 μm and were encased in a 410 × 330 μm capsule. Development appeared to be synchronous within the mass until approximately 30–32 days after oviposition. Cleavage, gastrulation, and development of the veliger follow the same pattern as described in *Haloa japonica* Pilsbry (Usuki, 1966), a closely related species with lecithotrophic development. The chronology of major developmental events is summarized in Table I and illustrated in Figures 2–6. Well developed veligers, with lengthened propodia, rhythmic contractions of the heart, and capable of complete retraction into the shell are visible in the egg masses 29 days after oviposition (Fig. 3). Hatching began approximately 3 days later. Some individuals from each egg mass hatched as veligers (Fig. 4), but the majority metamorphosed within the egg capsule (Fig. 5) and hatched as juveniles.

A few days before the onset of hatching, the jelly mass began to deteriorate and was colonized by diatoms and nematodes, as has been described for opisthobranch egg masses (Davis, 1967). Hatching generally occurred over a period lasting from 3 to 11 days. At hatching, capsule walls softened (*i.e.*, became flexible and readily distorted) and were eventually split by the larval propodium, allowing the individual to escape. This process took approximately 1.5 to 2 min after the first visible softening of the capsule. After the larva emerged from the capsule, it slowly worked its way out of the jelly mass. Veligers would then swim away, while juveniles often remained on the deteriorating mass or crawled to filaments of *Chaetomorpha* if available. Hatching of both veligers and juveniles occurred in the same way.

Hatched veligers did not grow during the pelagic period: shells remained 360 ± 16 × 280 ± 10 μm in size (veliger length 420 μm including extended velum) throughout the pelagic period (measured as by Hurst, 1967). Morphological changes other than decreasing yolk reserves were not visible. Neither the presence of

Table I

Summary of developmental events in Haminoea callidegenita *for egg masses cultured at 15°C*

Time (h, days)	Developmental event
0 h	Oviposition
24 h	First cleavage (holoblastic and equal)
46 h	Second cleavage
6 days	Blastula
7–8 days	Gastrula
10 days	Cephalopedal rudiment visible
12 days	Cilia and shell material appear, embryos irregularly rotating in capsules
13 days	Foot and velar lobes separate, shell growth over posterior quarter of yolk mass, regular rotation of embryos in capsules
14 days	Velum bilobed, cilia capable of beating metachronically
15 days	Operculum beginning to appear, ciliary beating can be arrested for short periods
16 days	Operculum present, shell growth to base of cephalopedal rudiment and separate from digestive glands, embryos rotating slowly (filling most of the capsules) and can change direction of rotation
18 days	Statocysts visible, 2 digestive glands distinct, shell curved 90° to larval right, body whorl of shell rounded
20 days	Eyes visible
21 days	Appearance of propodium
22 days	Esophagus and intestine visible, flexion of velar lobes, propodial thickening visible
25 days	Stomach visible, heart coelescing, complete retraction of larvae if disturbed by bright lights or water movements
29 days	Heart contracting, anus visible
32–39 days	Metamorphosis and/or hatching

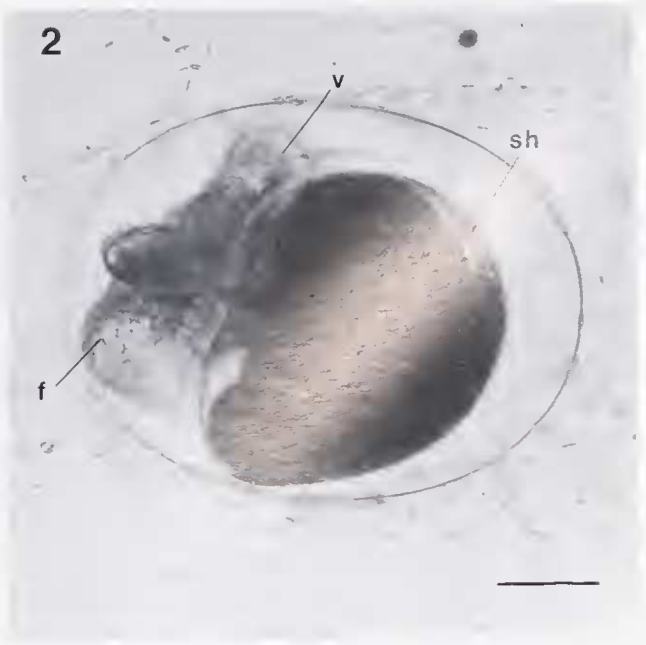

Figure 2. Photomicrograph of a 16-day *Haminoea callidegenita* veliger, also showing diatoms in the egg mass jelly (15°C). Scale = 90 μm. Legend: f-foot; sh-shell; v-velum.

unicellular algae in the gut nor the uptake of pigment by the digestive gland were evident, indicating that these veligers did not ingest food particles, as is known to occur in some other lecithotrophic veligers (Thompson, 1958; Kempf and Hadfield, 1985). *H. callidegenita* veligers were poor swimmers in culture conditions and periodically rested on algae and the bottom of the culture dish. Some veligers metamorphosed within 24 h of hatching, others remained pelagic for up to 20 days, when they successfully completed metamorphosis (5% mortality).

The majority of veligers metamorphosed within the capsule and hatched as juveniles. At metamorphosis, velar cilia were lost, the propodium elongated anteriorly, and the velar lobes gradually resorbed (Fig. 5). The larval shell was retained. Hatching occurred as described for extracapsular metamorphosis. Within 24 h of hatching, the foot lengthened posteriorly, and the operculum was cast off. As the remnants of the velar lobes were gradually resorbed, the cephalic lobe buds began to form on the posterior part of the head. Also, the orientation of the shell began to shift towards that of the adult, so the center of the aperture became positioned slightly to the right of the head.

Metamorphosis of individuals hatched as veligers occurred as described for intracapsular metamorphosis. Veliger and juvenile morphologies were the same for both encapsulated and hatched veligers.

All juveniles had sufficient (although decreasing) yolk reserves to allow several days delay in the onset of feeding. If food was available, juveniles usually began feeding within 24 h of metamorphosis, as indicated by the digestive glands becoming brown. Juveniles were epiphytic and particle grazers as were the adults. The buccal mass, radula, salivary glands, gizzard, and gizzard plates were visible and functional 4 days post-metamorphosis. Feeding setae, as described by Berrill (1931) in *H. hydatis* Linne, were not observed. Newly metamorphosed juveniles had resorbed most of the velar lobes and flattened the foot to extend anteriorly to project slightly in front of the head and posteriorly to the edge of the aperture. Rapid shell growth on the left side of the juvenile projected the shell posteriorly along the aperture. Thus, the overall shape changed from the veliger coil to a longer shell with an elongate aperture (Fig. 6). Growth of the foot was evident along the flaring of the aperture and, approximately 10 days after metamorphosis, the posterior pallial complex began to project beyond the body whorl of the shell. Animals become sexually mature when approximately 13 mm in length.

Induction of intracapsular metamorphosis

There was considerable variation in the relative proportions of veligers and juveniles hatching from egg masses cultured under identical conditions (Fig. 7). The percentage of total hatchlings (all hatchlings released from one egg mass throughout the entire hatching period) that emerged as veligers varied from 9.02% to 71.57% in 9 egg masses, although most masses fell within the 30–50% range. The mass with the smallest veliger component (9%; mass #5 in Fig. 7) was a medium sized mass (approximately 400 hatchlings) and hatching occurred over a relatively long period of time (10 days). The mass with the largest veliger component (70%; mass #7 in Fig. 7) was a large mass (approximately 600 hatchlings) and hatching occurred over a short period (3 days). Only one other mass had a 3-day hatching period (mass #6 in Fig. 7); approximately 40% of the hatchlings emerged as veligers from this mass. Mass #6 was also very small (150 hatchlings).

From each egg mass, hatching occurred over several days (Fig. 7). The relative proportions of veligers and juveniles changed throughout this period, with the percentage of veligers decreasing (Fig. 8) and the percentage of juveniles increasing with time, as would be expected as the juveniles represent a later stage of development. However, all egg masses had some juveniles emerging on the first day of hatching and some veligers hatching throughout most of the hatching period. Our estimation of the juvenile component is probably slightly high as observations were made every 24 h, and hatched veligers have been observed to metamorphose within this time interval. Despite a few days variation in the onset of hatching among masses, the same distribution of hatching stages was evident among individual masses.

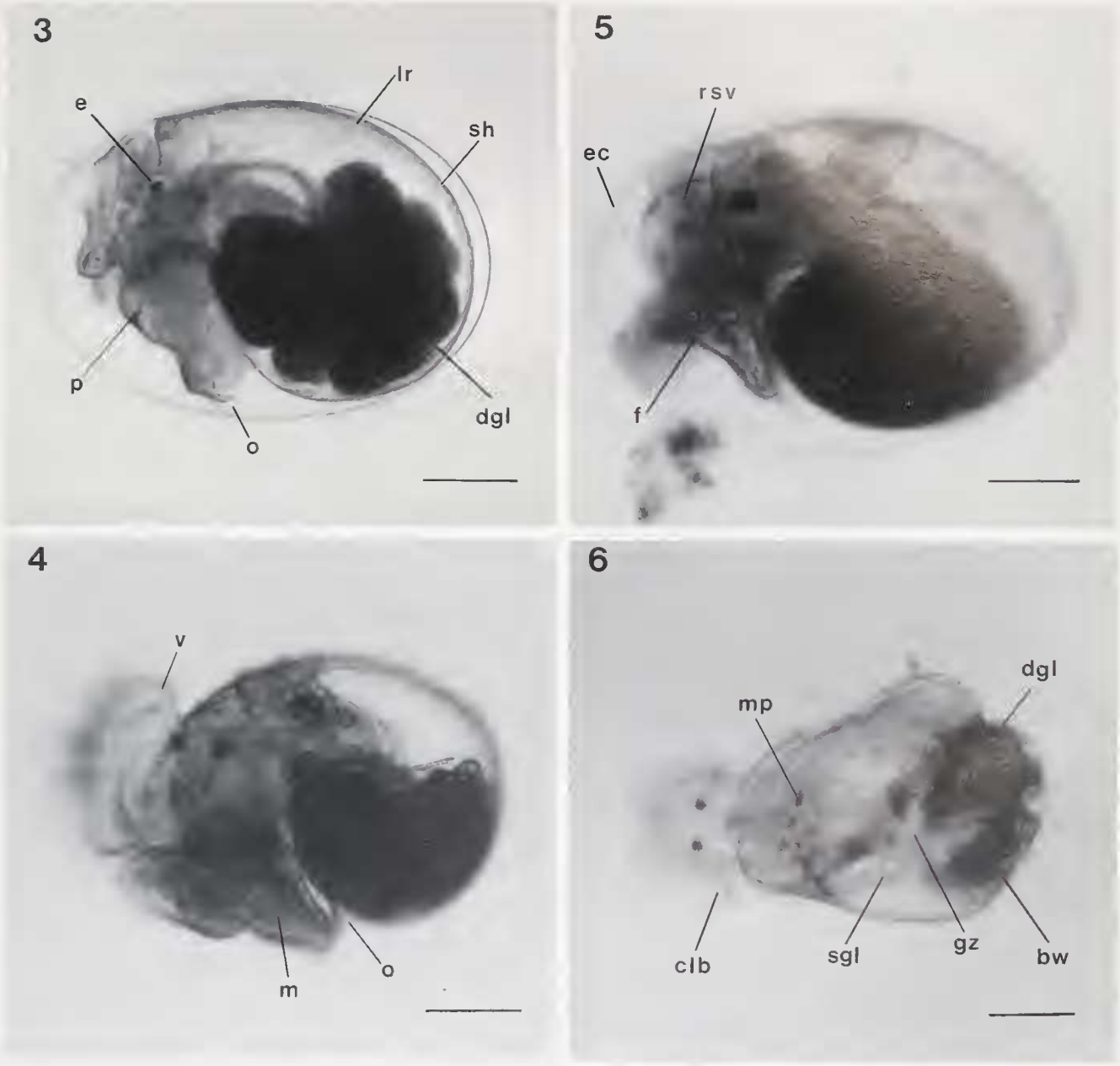

Figure 3–6. Photomicrographs of *Haminoea callidegenita* veligers and juveniles. Age is listed in days (d) for animals cultured at 15°C: (3) veliger, 29 d, scale = 100 μm; (4) veliger, 1 d hatched (31 d after oviposition), scale = 100 μm; (5) encapsulated juvenile, 32 d, scale = 100 μm; (6) juvenile, 10 d post-metamorphosis, scale = 300 μm. Legend: bw-body whorl of shell; clb-cephalic lobe bud; dgl-digestive gland; e-eye; ec-embryonic capsule; f-foot; g-gizzard; lr-larval retractor muscle; m-metapodium; mp-mantle pigment; o-operculum; p-propodium; rsv-partially resorbed velum; sgl-salivary gland; sh-shell; v-velum.

It is possible that in opisthobranch egg masses, the jelly may influence oxygen diffusion so that O_2 tension is lower in the center of an egg mass than at the periphery, thus slowing the rate of development of the central embryos. As *H. callidegenita* produce thick, cylindrical egg masses, and as the egg string is irregularly deposited in each jelly mass, we thought the distance between embryo and egg mass surface may be influential in determining the rate of development and therefore the hatching stage. The effect of decreasing the jelly thickness around developing embryos was determined by examining the percent veligers hatching daily from intact egg masses, masses cut in 2-mm thick slices, and encapsulated embryos removed from the mass jelly. Encapsulated embryos could be raised successfully without the jelly mass; there was a 100% success rate in hatching of healthy veli-

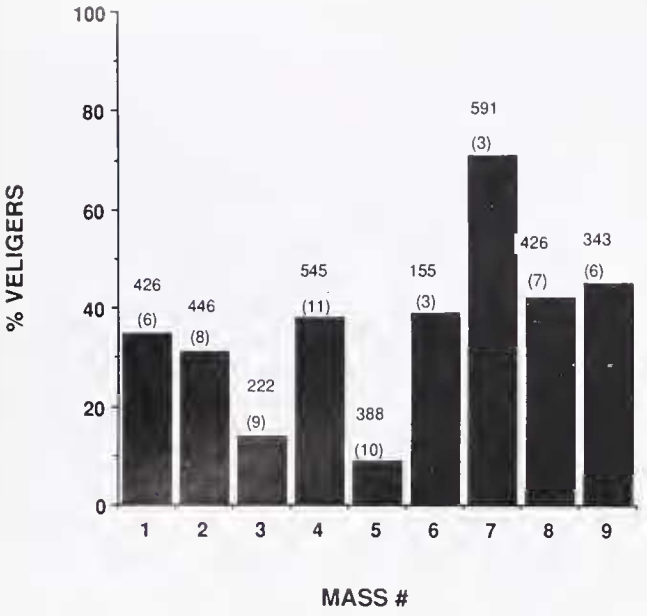

Figure 7. Hatching in *Haminoea callidegenita* egg masses: values plotted are the percent of total hatchlings per mass that emerged as veligers (n = 9 egg masses; 15°C). Numbers above each bar are total number of hatchlings per mass (top number) and duration of the hatching period in days (in brackets).

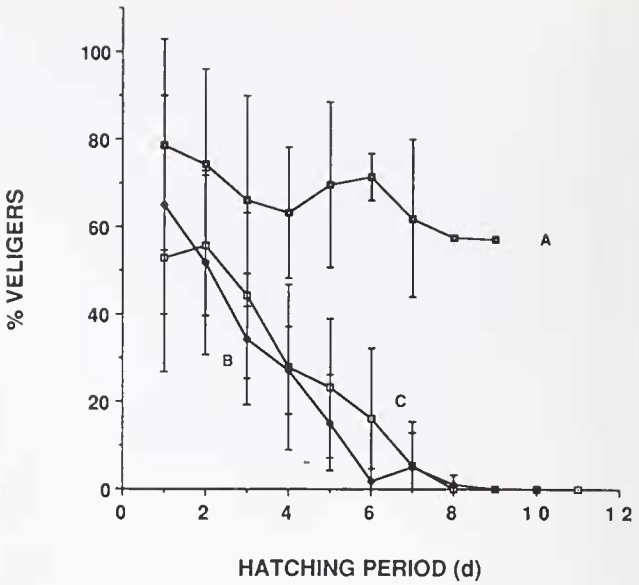

Figure 9. Effects on the hatching stage of removing egg mass jelly from *Haminoea callidegenita* embryos. Values plotted are means plus standard error bars for the percent daily hatchlings that emerged as veligers on each day of the hatching period, for three treatment groups (15°C): (A) embryos separated from the egg mass (n = 10 cultures); (B) egg mass slices (n = 10); and, (C) entire egg masses (n = 9).

gers and juveniles, which proceeded to metamorphose (in the case of the hatched veligers) and grow at the expected laboratory rate (0.02 mm/day). Intact egg masses and mass slices showed approximately the same percentage of veligers released throughout the hatching period (Fig. 9). Veligers represented 60% of the hatchlings at the onset of hatching (day 1), decreasing to 5% on day 7, and 0% by the end of the hatching period (*i.e.*, all hatchlings emerged as juveniles on the last day of hatching). Veligers hatching from capsules separated from the egg mass jelly represented approximately 80% of the hatchlings at the onset of hatching, and this rate remained relatively consistent throughout the hatching period, decreasing to 65% on the last day of hatching (day 9).

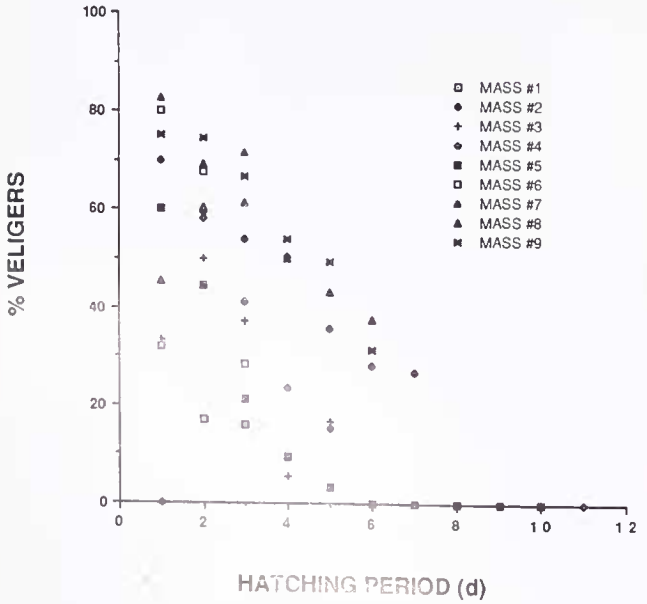

Figure 8. Distribution of developmental stages at hatching in *Haminoea callidegenita* plotted as the percent daily hatchlings that emerged as veligers throughout the hatching period (time in days; 15°C). Each symbol represents a different egg mass (n = 9 egg masses).

Embryos separated from the egg mass jelly were placed under three culture conditions: control (seawater only), seawater plus *Chaetomorpha*, and seawater plus pieces of egg mass jelly. Isolated embryos showed a distribution of hatching stages similar to that of the previous experiment (Fig. 10): 95% of the hatchlings were veligers on the first day of hatching, decreasing to 75% on the last day (day 5). Embryos cultured in the presence of *Chaetomorpha* showed similar results (73% released as veligers on day 1 of hatching, and 85% on the last day, day 4). However, embryos cultured in water containing egg mass jelly followed the same pattern as did hatchlings released from intact egg masses: 72% hatched as veligers on day 1, decreasing to 0% on day 6, the last day of the hatching period.

Induction of extracapsular metamorphosis

Extracapsular metamorphosis was examined in veligers which hatched from intact egg masses to see if the

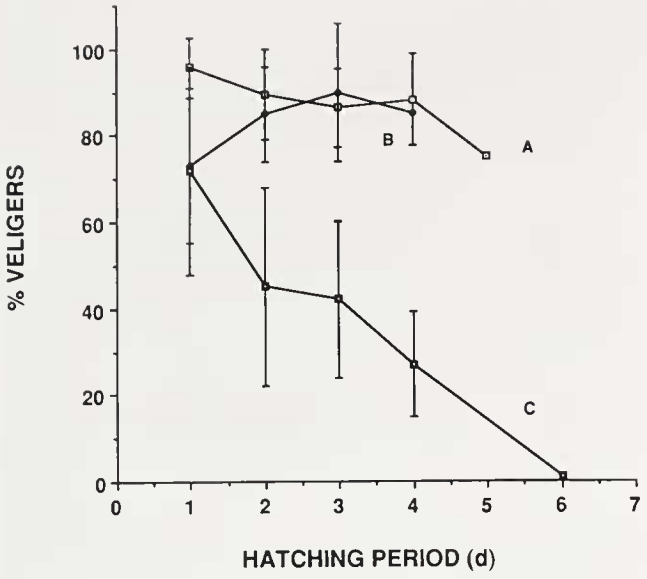

Figure 10. Effects of culturing separated embryos in the presence of: (A) seawater only (n = 10 cultures); (B) seawater plus *Chaetomorpha linum* (n = 10); and (C) seawater plus egg mass jelly pieces (n = 10). Values plotted are means plus standard error bars for each day of the hatching period.

rate of metamorphosis could be enhanced by substrata collected from the adult habitat. Three substrata were tested, all of which were frequently observed in association with small juveniles in Spencer's Spit: *Chaetomorpha*, silt, and egg mass jelly. Metamorphosis occurred under all of these conditions (Fig. 11). The presence of *Chaetomorpha* and egg mass jelly enhanced the rate of metamorphosis such that it took 9 days for all veligers to successfully metamorphose (2.90% and 0.00% mortality, respectively), rather than 20 days as in the control conditions (5.00% mortality). Veligers provided with silt as a substratum showed 5.70% mortality.

Discussion

The development of *Haminoea callidegenita* is morphologically similar to that described for *Haloa japonica* (Usuki, 1966), another cephalaspidean species, and to lecithotrophic opisthobranchs in general (Thompson, 1967). However, the timing of metamorphosis in *H. callidegenita* is variable: veligers can metamorphose within the egg capsule or after hatching. This unusual pattern has the adaptive advantage of allowing immediate recruitment within a population while simultaneously allowing larval dispersal. However, the prominence of pelagic veligers of this species in its natural habitat has not yet been determined (Gibson and Chia, in progress).

The percent of total hatchlings that emerged as veligers was variable among masses cultured simultaneously under identical conditions. Although mass size (ranging from 155 to 591 hatchlings/mass) and duration of the hatching period (from 3 to 11 days) may have influenced the percentage of veligers hatching from a particular mass, it seemed that there was a greater variance than could be accounted for by only these two components. Each of the masses examined were produced by different individuals; whether the observed variance is genetically influenced has not yet been examined.

The thickness of the jelly layer surrounding the embryos did not affect hatching stage (whole *vs.* sliced masses). However, embryos that were isolated from the egg mass jelly showed a high percentage of individuals hatching as veligers, and throughout the hatching period this percentage did not decrease as much as would be expected from a comparison with percentages obtained from intact egg masses. In addition, culturing embryos in the presence of mass jelly produced percentages of intra- and extracapsular metamorphosis as seen in intact egg masses. This suggests that either the egg mass jelly or something associated with the jelly promotes intracapsular metamorphosis of some, but not all, individuals. Direct contact between capsule and egg mass jelly is not required to induce metamorphosis, indicating that the inducing factor is a diffusible chemical. However, the chemical nature of this compound is yet to be determined (Gibson and Chia, in progress).

Chaetomorpha linum provided the surface most commonly grazed for epiphytes by *H. callidegenita* juveniles and adults. The presence of *Chaetomorpha* did not increase the rate of intracapsular metamorphosis. However, the rate of metamorphosis of individuals that

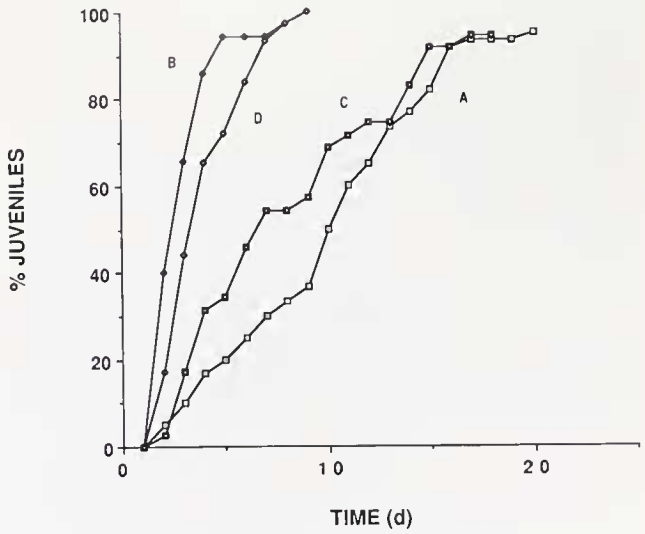

Figure 11. Extracapsular metamorphosis of *Haminoea callidegenita* expressed as the number of individuals that had successfully completed metamorphosis by the indicated day, as a percent of the original number of veligers per substratum. Substrata: (A) seawater only (n = 12 cultures); (B) *Chaetomorpha linum* (n = 7); (C) sediment (n = 7); (D) egg mass jelly (n = 15).

hatched as veligers was enhanced by the presence of *Chaetomorpha* indicating that the factor in *Chaetomorpha* influencing metamorphosis of *H. callidegenita* differs from that of the egg mass jelly.

H. callidegenita veligers were potentially competent to metamorphose over a long period. Some individuals will metamorphose within the egg capsule. The factor(s) which determine which individuals will metamorphose before hatching are unknown, possibly variable sensitivities of the embryos themselves. However, these factors appear to be influenced by egg mass jelly, causing metamorphosis. Other individuals will metamorphose shortly after hatching (1–3 days) if they encounter a favorable substratum, such as a juvenile food source. Still other individuals will delay metamorphosis for 20 days after hatching (potentially longer), until appropriate conditions are met. *H. callidegenita* veligers appear to become increasingly sensitive to metamorphic cues during their development, as veligers hatched from intact egg masses metamorphose in response to jelly pieces, even though jelly before hatching did not provide a strong enough stimulus.

Acknowledgments

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Literature Cited

Bickell, L. 1978. Larval development, metamorphosis, and juvenile feeding of *Doridella steinbergae* (Lance) (Opisthobranchia: Nudibranchia). M. Sc. Thesis, University of Alberta. 226 pp.

Berrill, N. J. 1931. The natural history of *Bulla hydatis* Linne. *J. Mar. Biol. Assoc. U.K.* **17**: 567–571.

Bonar, D. B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. Pp. 177–196 in *Settlement and Metamorphosis of Marine Invertebrate Larvae*, F. S. Chia and M. Rice, eds. Elsevier, New York.

Bridges, C. B. 1975. Larval development of *Phyllaplysia taylori* Dall, with a discussion of development in the Anaspidea (Opisthobranchia: Mesogastropoda). *Ophelia* **14**: 161–184.

Chia, F. S. 1971. [illegible] fecundity, and larval development of three sacoglossan opisthobranchs from the Northumberland coast, England. *Veliger* **13**(4): [illegible]

Chia, F. S., and R. K. Koss. 1978. Development and metamorphosis of the planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). *Mar. Biol.* **46**: 109–119.

Clark, K. B., and A. Goetzfried. 1978. Zoogeographic influences on developmental patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *J. Moll. Stud.* **44**: 283–294.

Clark, K. B., M. Busacca, and H. Stirts. 1979. Nutritional aspects of development of the ascoglossan *Elysia cauze*. Pp. 11–24 in *Reproductive Ecology of Marine Invertebrates*, S. E. Stancyk, ed. University of South Carolina Press, Columbia.

Davis, C. C. 1967. Emergence of veliger larvae from eggs in gelatinous masses laid by some Jamaican marine gastropods. *Malacologia* **5**(2): 299–309.

Eyster, L. S. 1979. Reproduction and developmental variability in the opisthobranch *Tenellia pallida*. *Mar. Biol.* **51**: 133–140.

Gibson, G. D., and F. S. Chia. 1989. Description of a new species of *Haminoea*, *Haminoea callidegenita* (Mollusca: Opisthobranchia), with a comparison with two other *Haminoea* species found in the Northeast Pacific. *Can. J. Zool.* **67**.

Hoagland, K. E., and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? *Biol. Bull.* **174**: 109–125.

Hurst, A. 1967. The egg masses and veligers of thirty Northeast Pacific opisthobranchs. *Veliger* **9**: 255–288.

Kempf, S. C., and M. G. Hadfield. 1985. Planktotrophy by the lecithotrophic nudibranch, *Phestilla sibogae* (Gastropoda). *Biol. Bull.* **169**: 119–130.

Morton, J. E. 1979. *Molluscs*. Hutchinson and Company, London. 244 pp.

Purchon, R. D. 1977. *The Biology of the Mollusca*, 2nd edition. Pergamon Press, New York. 560 pp.

Rao, K. V. 1961. Development and life history of a nudibranchiate gastropod *Cuthona adyarensis* Rao. *J. Mar. Biol. Assoc. India.* **3**(1): 186–197.

Smith, S. T. 1967. The development of *Retusa obtusa* (Montagu) (Gastropoda: Opisthobranchia). *Can. J. Zool.* **45**: 737–763.

Switzer-Dunlap, M., and M. G. Hadfield. 1977. Observations on development, larval growth and metamorphosis of four species of Aplysiidae (Gastropoda: Opisthobranchia) in laboratory culture. *J. Exp. Mar. Biol. Ecol.* **29**: 245–261.

Thompson, T. E. 1958. The natural history, embryology, larval biology, and post-larval development of *Adalaria proxima* (Alder and Hancock) (Gastropoda: Opisthobranchia). *Phil. Trans. R. Soc. Lond. B.* **242**: 1–57.

Thompson, T. E. 1967. Direct development in a nudibranch *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. U.K.* **47**: 1–22.

Usuki, I. 1966. The life cycle of *Haloa japonica* (Pilsbry). *Sci. Rep. Niigata Univ. D (Biol.)* **3**: 87–105.

West, H. H., J. Harrigan, and S. Pierce. 1984. Hybridization of two populations of a marine opisthobranch with different developmental patterns. *Veliger* **26**(3): 199–206.

Williams, L. G. 1980. Development and feeding of larvae of the nudibranch gastropods *Hermissenda crassicornis* and *Aeolida papillosa*. *Malacologia* **20**(1): 99–116.